

McClanahan, T. R., V. Hendrick, M. J. Rodrigues, and N. V. C. Polunin. 1999. Varying responses of herbivorous and invertebrate-feeding fishes to macroalgal reduction on a coral reef. *Coral Reefs* 18: 195-203.

Ogden, J. C. 1976. Some aspects of herbivore-plant relationships on Caribbean reefs and seagrass beds. *Aquatic Biology* 2: 103-116.

Pitcher, T. J., A. E. Magurran, and I. J. Winfield. 1982. Fish in larger shoals find food faster. *Behavioral Ecology and Sociobiology* 10: 149-151.

Pitcher, T. J. and A. E. Magurran. 1983. Shoal size, patch profitability and information exchange in foraging goldfish. *Animal behavior* 31: 546-555.

Thresher, R. E. 1980. Reef Fish: Behavior and ecology of the reef and in the aquarium. Palmetto Publishing Company: St Petersburg, FL.

RESOURCE PARTITIONING AMONG THE ACANTHURIDS *ACANTHURUS CHIRURGUS* AND *ACANTHURUS BAHIANUS* AT DISCOVERY BAY, JAMAICA

KATHERINE W. MANARAS, LINDA E. AUCOIN, ZOË M. McLAREN, AND ASHLEY C. BROWN

Abstract: Species with overlapping niches often partition resources in order to reduce inter-specific competition. Two herbivorous species of acanthurids, ocean surgeons (*Acanthurus bahianus*) and doctor fish (*A. chirurgus*) appear to have overlapping resource needs in the coral reefs of Discovery Bay, Jamaica. We examined whether these two species partitioned resources in order to avoid interactions and reduce competition. We found that these fish exhibited spatial partitioning, with more doctor fish occurring in shallow waters and more ocean surgeons at depths below 5 m. In the shallow depths, *A. bahianus* and *A. chirurgus* tended to school with both congeners and other species, while at deeper depths, individuals tended to be in schools with only other species, i.e. without congeners. The dominant food type observed in 15 s observation periods did not differ between the two species. Thus, our results indicate that resource partitioning between ocean surgeons and doctor fish occurs via spatial distribution but not necessarily through food preferences. Our results also suggest there are different schooling patterns for both species at different depths, possibly because there is decreased pressure to avoid congeneric interactions in shallow depths where food resources may be more abundant. The intricacies of the relationships between species with closely overlapping niches contributes to understanding the high diversity of coral reef fish assemblages.

Key Words: doctor fish, herbivory, interspecific competition, ocean surgeon fish, schooling

INTRODUCTION

Interference competition between tropical reef fish has been demonstrated to structure habitat use in species whose niches overlap (Robertson and Gaines 1986). The greater the overlap in distribution or foraging habits, the more intense the competition will be, especially when resources are limiting. Two species of acanthurids, ocean surgeons (*Acanthurus bahianus*) and doctor fish (*A. chirurgus*), are both herbivores which feed mainly on macroalgae, but also diatoms and microalgae found in sediment (Barlow 1974). Although commonly geographically isolated (Thresher 1980), they locally co-occur in Discovery Bay, Jamaica. While interspecific aggression can be intense within this family (Robertson and Gaines 1986), research suggests that these interactions can be minimized by partitioning resources in a variety of ways. Acanthurids may reduce interactions by reef-wide spatial distribution. Additionally, be-

cause they have very similar food preferences (Earle 1972), acanthurids may be able to reduce interspecific aggression by schooling with non-congeneric species, i.e. schools with other than ocean surgeons or doctor fish, such as parrot fish and wrasses.

We hypothesize that ocean surgeons and doctor fish should partition spatial and food resources and minimize social encounters in schools. Specifically, (a) ocean surgeons and doctor fish should be found at different depths, (b) both species should school more often in mixed-species schools with non-congeners than those with congeners, and (c) the feeding habits of both species should differ in order to reduce interspecific competition for food resources.

METHODS

From 6-9 March 2000 we collected data near the LTS site of Discovery Bay, Jamaica. To determine the frequency of different

schooling types and the abundance of acanthurids at different depths, we swam eight 5-min transects at each of eight depths: on the back reef at 1–3 m, on the reef crest at 0–1 m, and six 2-meter intervals on the fore reef from 1–10 m. Transects were 2-m wide and followed the contour line of the reef. Every ocean surgeon and doctor fish occurring in each transect was noted, along with the composition of the group with which it was associated. School categories were: alone, mixed-species schools with congeners (i.e. either one or more individuals of the same species or same genus in the school), and mixed-species schools with non-congeners (i.e. one individual of one species of Acanthuridae in the school of other species, such as parrotfish and wrasses).

To determine the feeding habits of *A. bahianus* and *A. chirurgus* at the different depths and within the various school types, two divers surveyed each depth for approximately 40 minutes, recording one observation of aggregation type and feeding activity per species per school type encountered. We used the same school types as in transect surveys, and we described feeding activity as both the number of bites taken over a 15-s observation period and the dominant food type (that which received the majority of bites). We classified the foraging substrate as Dictyotidae algae, microalgal turf, Halimedaceae algae, all other macroalgae, epiphytes upon *Thalassia testudinum*, or sand. Each 15 s observation period began when the diver observed a fish beginning to feed.

We used contingency analysis to examine the relationship between the total number of individuals in each species at each of the 2 m depth intervals. Because we observed a sharp distinction between abundances in depths greater than or less than 5 m, we grouped all data accordingly, and analyzed the effects of species on school type and dominant food types within shallow depths (< 5 m

deep) and deep depths (> 5 m deep). We examined the relationships between the number of *A. bahianus* and *A. chirurgus* found in each of three school types for each depth group. We also compared the diets (defined by the percentages for each food substrate occurring as the dominant food type) of each species for both shallow and deep depths. Additionally, the mean numbers of bites per observation period were compared among the different school types for *A. bahianus* and *A. chirurgus* using an ANOVA.

RESULTS

The abundance of ocean surgeons and doctor fish varied with depth; more doctor fish than ocean surgeons were found in the fore reef in depths shallower than 5 m, and more ocean surgeons than doctor fish were found at all depths deeper than 5 m (Figure 1). In 64 transects, we made 275 observations of acanthurids schooling or swimming alone: 77 observations were of lone individuals, and 198 were of schools with one or more acanthurids. There was no difference in the abundances of acanthurids between shallow and deep depths ($t = 1.624$, $df = 6$, $p = 0.156$).

There was no significant relationship between species and school type (alone, school with congeners, mixed school with non-congeners) in either the shallow (< 5 m) or the deep (> 5 m) depths (shallow: $G = 3.178$, $df = 2$, $p = 0.204$; deep: $G = 0.13$, $df = 2$, $p = 0.939$). Acanthurids were more likely to be found in schools with non-congeners in deep depths, and in schools with congeners in shallow depths (Figure 2).

The overall diet of ocean surgeons and doctor fish did not differ from one another in either shallow or deep depths (shallow: $G = 7.00$, $df = 5$, $p = 0.156$; deep: $G = 3.02$, $df = 4$, $p = 0.555$). The majority of the acanthurids' diet was composed of Dictyotidae in the shallow depths, while the majority of their diet was

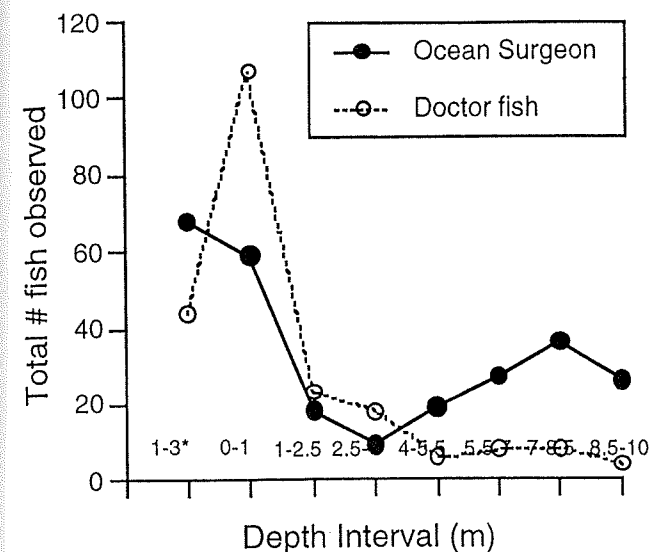


Figure 1. Total number of *Acanthurus bahianus* and *A. chirurgus* observed in eight five-minute transects at each of eight depths. Transects were conducted in the fore reef and adjacent back reef at the LTS site, Discovery Bay Marine Laboratory, Jamaica. 1-3* depth interval corresponds to this depth (m) in the back reef, 0-1 m depth interval corresponds to the reef crest, and all other intervals correspond to depths in the fore reef.

composed of Dictyotidae and microalgal turf in the deep depths (Figure 3).

The mean number of bites taken by a fish in a 15 s period was greater when fish were alone or in schools with non-congeners (9.31 ± 0.76 and 10.92 ± 0.53 , respectively) than when fish were in mixed schools with congeners (6.74 ± 0.47) ($x \pm SE$, F_4 , $269 = 17.74$, $p < 0.0001$).

DISCUSSION

Our results demonstrated spatial partitioning between *A. bahianus* and *A. chirurgus*. Abundances were similar in the shallow depths, but ocean surgeons dominated in the deeper depths, corresponding to past studies that found doctorfish in shallower waters than ocean surgeons (Thresher 1990).

Both species of Acanthuridae appeared to use schools to partition resources in the deeper depths, where individual ocean sur-

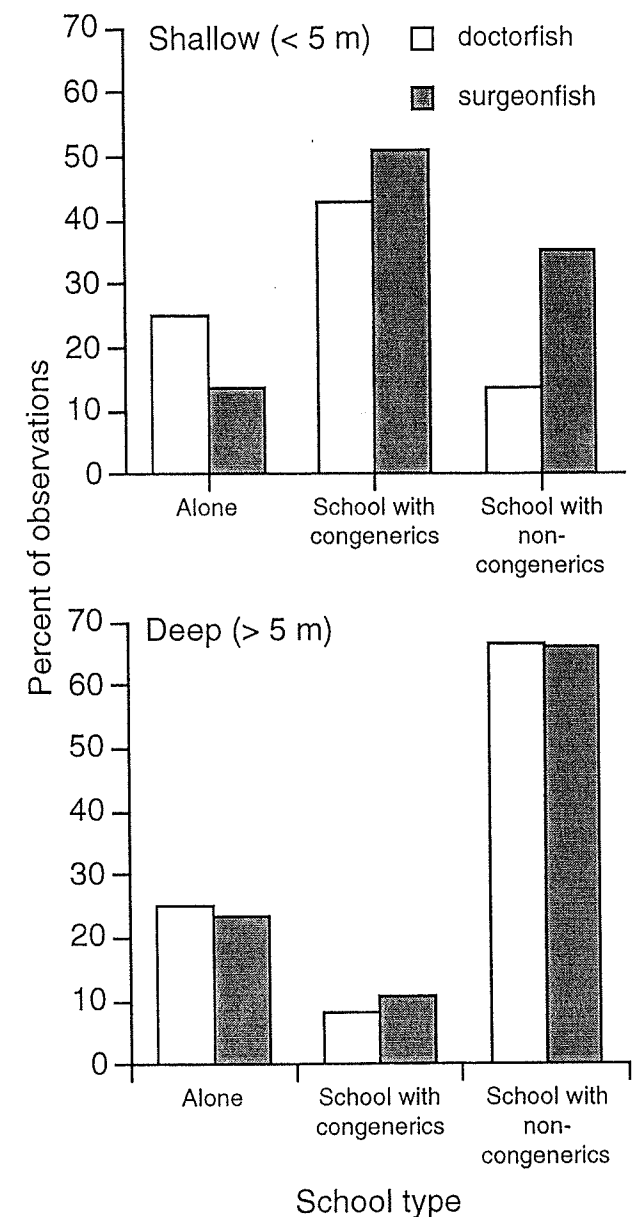


Figure 2. Comparison between school type (fish occurring alone, in mixed-species schools with congeners, and in mixed-species schools with non-congeners) in the percent of total observations recorded during 15 s observation periods of ocean surgeons and doctor fish in Discovery Bay, Jamaica.

geons and doctorfish spent a greater percentage of their time in mixed-species schools without congeners. This behavior may be advantageous because limited resources in the deeper depths could amplify intra-generic competition. Algal resources may be less at

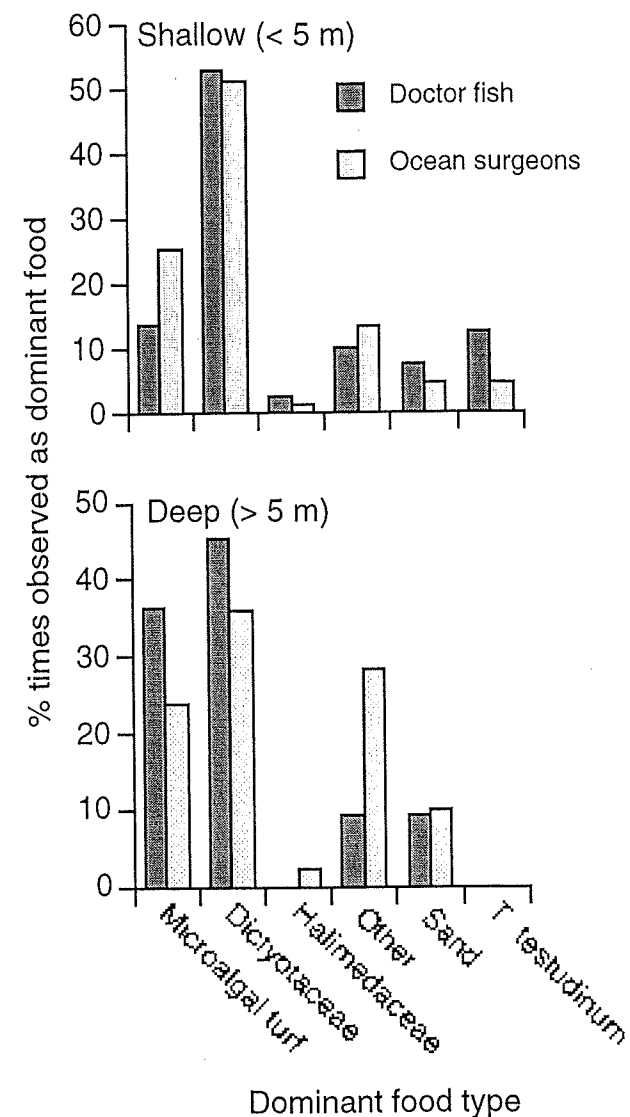


Figure 3. Dominant food types of doctor fish and ocean surgeons in deep (> 5 m) and shallow (< 5 m) water from 90 observations of doctor fish and 192 observations of ocean surgeons feeding in Discovery Bay, Jamaica.

deeper depths due to less light or different species compositions. Thus, doctor fish and ocean surgeons would attempt to increase their fitness by reducing the time spent foraging in direct competition with congeners.

In the shallower depths, the high percentage of schooling with congeners by both species may be attributed to a reduction in intensity of competition. If resources are more abundant in the shallow waters, ocean surgeons and doctorfish may not need to avoid

each other in order to co-exist. Further study could examine the abundance of food in deeper depths compared with shallow.

Alternatively, fish could be less likely to school with congeners in deeper depths if fish abundances were lower. Foster (1987) demonstrated that fish are less likely to school at lower densities. Low total abundances of congeners in a habitat may affect schooling behavior by reducing the encounter rate between congeners. However, abundance, and therefore encounter rates, were found to be constant between deep and shallow depths in this study. Thus this theory does not appear to explain the differences we observed.

Contrary to our hypothesis, we found no evidence for resource partitioning by food type. The similar diets of doctorfish and ocean surgeons suggest that neither species excludes the other from a preferred food source, or that competition has not led to food niche partitioning. Thus, partitioning of resources appears to occur only through spatial mechanisms in the two species.

Foster (1985) indicates that, in certain cases, reduced competition for food is not a major advantage of mixed species schools. Instead, schooling in areas where damselfish territories maintain many algal resources may benefit all members of a school, regardless of competition. Damselfish territories were relatively abundant in all of our sites, and gaining access to these high-resource areas may be more important than possible intra-generic competition in ocean surgeon and doctor fish.

Thus, our study suggests these species of the Acanthuridae use depth to spatially partition resources, choose to participate in schools with varying compositions at different depths, and do not seem to have different diets. Elucidating foraging patterns of reef fish, especially of species with significant niche overlap such as ocean surgeons and doctor fish, contributes to an understanding of the high diversity of coral reef assemblages.

LITERATURE CITED

- Barlow, G. W. 1974. Contrasts in social behavior between Central American cichlid fishes and coral-reef surgeonfishes. *American Zoologist* 14: 34.
- Debrot, A. O. and A. A. Myrberg, Jr. 1988. Intraspecific avoidance as a proximate cause for mixed-species shoaling by juveniles of a western Atlantic surgeonfish, *Acanthurus bahianus*. *Bulletin of Marine Science* 43: 104-106.
- Earle, S. A. 1972. The influence of herbivores on the marine plants of great Lameshur Bay, with an annotated list of plants. Natural History Museum of Los Angeles County, Los Angeles, California.
- Foster, S. A. 1985. Group foraging by a coral reef fish: a mechanism for gaining access to defended resources. *Animal Behavior* 33: 782-792.
- Foster, S. A. 1987. Acquisition of a defended resource: a benefit of group foraging for the neotropical wrasse, *Thalassoma lucasanum*. *Environmental Biology of Fishes* 19: 215-222.
- Hall, K. 1988. An observational study of surgeonfish feeding behavior. *Dartmouth Studies in Tropical Ecology*. Dartmouth College. Hanover, NH.
- Pitts, P. A. 1991. Comparative use of food and space by three Bahamian butterflyfishes. *Bulletin of Marine Science* 48: 749-756.
- Robertson, D. R. and S. D. Gaines. 1986. Interference competition structures habitat use in a local assemblage of coral reef surgeonfishes. *Ecology* 67: 1372-1383.
- Robertson, D. R., H. P. A. Sweatman, E. A. Fletcher and M. G. Cleland. 1976. Schooling as a mechanism for circumventing the territoriality of competitors. *Ecology* 57: 1208-1220.
- Thresher, R. E. 1980. Reef Fish: Behavior and ecology on the reef and in the aquarium. The Paletto Publishing Company: St. Petersburg, FL.